



# Royal Netherlands Academy of Arts and Sciences (KNAW) KONINKLIJKE NEDERLANDSE AKADEMIE VAN WETENSCHAPPEN

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### **published in**

Current Opinion in Plant Biology  
2021

### **DOI (link to publisher)**

[10.1016/j.pbi.2021.102025](https://doi.org/10.1016/j.pbi.2021.102025)

### **document version**

Publisher's PDF, also known as Version of record

[Link to publication in KNAW Research Portal](#)

### **citation for published version (APA)**

Song, C., Jin, K., & Raaijmakers, J. M. (2021). Designing a home for beneficial plant microbiomes. *Current Opinion in Plant Biology*, 62, Article 102025. <https://doi.org/10.1016/j.pbi.2021.102025>

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# Designing a home for beneficial plant microbiomes

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The plant microbiome comprises a highly diverse community of saprotrophic, mutualistic, and pathogenic microbes that can affect plant growth and plant health. There is substantial interest to exploit beneficial members of plant microbiomes for new sustainable management strategies in crop production. However, poor survival and colonization of plant tissues by introduced microbial isolates as well as lack of expression of the plant growth-promoting or disease-suppressive traits at the right time and place are still major limitations for successful implementation of microbiomes in future agricultural practices and plant breeding programs. Similar to building a home for humans, we discuss different strategies of building a home for beneficial plant microbiomes, here referred to as the 'MicrobiHome'.

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Current Opinion in Plant Biology 2021, 62:1–10

This review comes from a themed issue on **Biotic interactions**

Edited by **Jeffery L Dangl** and **Jonathan DG Jones**

<https://doi.org/10.1016/j.pbi.2021.102025>

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## Current strategies to engineer rhizosphere microbiomes

The rhizosphere is the interface between plant roots and soil, harboring diverse microbial communities with dynamic interactions and complex molecular cross talk [1,2,3<sup>\*</sup>,4,5]. Plant roots not just shape the rhizosphere microbiome but also modify the physicochemical properties of the surrounding soil [6,7]. Perturbation or engineering of plant root microbiomes can change plant fitness either directly or indirectly by changing their

microenvironment, leading to alterations in soil fertility [8,9]. A better understanding of these processes is critical for augmentation of beneficial members of indigenous rhizosphere microbiomes and for improving the functioning of introduced microbial strains and synthetic communities (SynComs).

Microbiome engineering requires integration of fundamental scientific knowledge of the taxonomic and functional diversity of the indigenous microbiome and quantitative design to create microbiomes that perform the desired functions, such as nutrient acquisition or enhanced tolerance to (a)biotic stresses [8,10]. To date, different strategies have been proposed to engineer soil and plant microbiomes, including i) microbiome transplantation, ii) introduction of single microbial strains or SynComs, iii) host-mediated recruitment and activation of specific beneficial microbiome members, and iv) engineering microbiomes via soil amendments such as addition of specific substrates that enhance growth and/or induce particular activities of beneficial microbiome members. This latter approach is referred to as the prebiotic approach in human microbiome research.

Transplantation of microbiomes is best exemplified in past and present studies on disease-suppressive soils where transferring small amounts of a suppressive soil into a non-suppressive (i.e. conducive) soil confers, at least in part, the disease suppressive phenotype (reviewed in Ref. [11]). Recently, Morella *et al.* [12<sup>\*\*</sup>] adopted a similar approach for the phyllosphere by successive passaging the leaf microbiome from one tomato plant to the next generation, thereby selecting for a robust and host-adapted microbiome. Although no microbiome-associated phenotypes (MAPs; [13]) were assessed in this study, the approach of successive microbiome passaging revealed the selection of a host-genotype independent microbiome over time. Considering that poor colonization of multiple host genotypes has been a major impediment in the successful application of microbial inoculants to date [14,15], this approach of successive passaging can be highly instrumental in selecting individual strains or SynComs that are better adapted at colonizing multiple host genotypes in competition with the indigenous microbiome. In the so-called MAPs-first approach, Oyserman *et al.* [13] further proposed strategies to design 'modular microbiomes', that is, synthetic microbial consortia that are engineered cooperatively with the host genotype to confer different but mutually compatible MAPs to a single host or host population. This approach of host-mediated microbiome selection also allows the identification of both plant and microbial genes that co-evolved,

fundamental knowledge that is still scarce but essential for the development of microbiome-based plant breeding strategies. In line with these studies is the design-build-test-learn (DBTL) cycle proposed by Lawson *et al.* [10], which integrates ecosystem level controls on selection of microbiomes with desired functions (top down), and predictions of how metabolic fluxes generate the desired network and microbial interactions (bottom-up). Knowledge of metabolic fluxes, that is, the dynamics of specific metabolites in root exudates, can be used in the design of a plant prebiotics approach where addition of substrates or precursors of biosynthetic pathways can selectively enrich for specific microbial species or trigger microbial activities that are beneficial for the plant host [16]. For example, Yang *et al.* [17] showed that the ratio of nitrogen and phosphorus affects the efficacy of a beneficial SynCom to resist invasion by plant pathogenic *Ralstonia solanacearum*. To date, however, there is still a large knowledge gap in the mechanistic understanding of how plant roots shape the microhabitats of their microbiomes [18]. The potential of plants to build a ‘home’ for root-associated microbes, here referred to as the MicrobiHome (Figure 1), will be discussed below.

### Designing a MicrobiHome Constructing a stable foundation

Root morphological and biochemical traits determine the explorative ‘behaviour’ of roots grown in the soil [7,19–21]. When roots penetrate the soil profile, exudates are released from the root surface to the surrounding soil [2,22,23], not only reducing the friction with the soil matrix but also adjusting soil moisture. There is growing evidence that certain root exudate components affect the rhizosphere microbiome by dispersion and gelling of soil [24] and by modulation of water and nutrient availability [25,26]. The root mucilage can improve stabilization of soil particles and facilitate the movement of microbes to the root surface [27,28,29]. In rhizosphere soil, mucilage, root border cells (RBCs) and their secretions form a functional entity and impact on soil microbes. RBCs have been shown to trap and immobilize zoospores of oomycete pathogens, to synthesize defensive structures in response to fungal attack, to repel pathogenic bacteria, and to control growth and gene expression in symbiotic bacteria [23,30–32]. Extending or reviving the experimental use of RBCs could be highly instrumental in understanding the yet unknown mechanisms of the cross-talk between plant root cells and the microbiome.

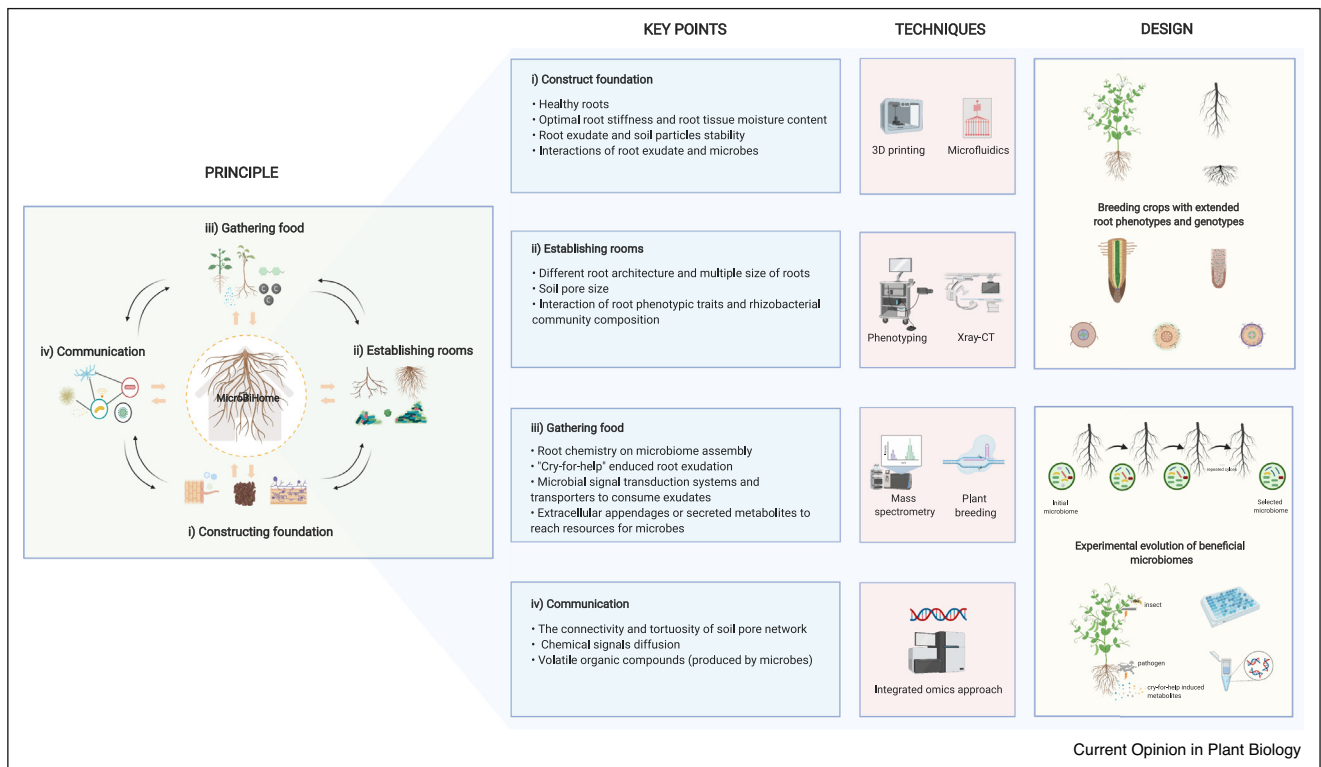
In addition to the effects of structural and chemical characteristics of plant roots on the microbiome, microbes themselves can induce root cell division and differentiation at both the meristem and at sites of lateral root formation [33]. For example, Cheng *et al.* [34] found that *Pseudomonas fluorescens* strain SS101 enhances lateral root formation of *Arabidopsis thaliana* and induces systemic resistance against the bacterial leaf pathogen *Pseudomonas*

*syringae* pv. *tomato* (*Pst*). Using sensitive and high-throughput assays to study microbe-associated molecular patterns (MAMPs) in *Arabidopsis* roots, Millet *et al.* [35] showed strong transcriptional responses and epidermal callose deposition in MAMP-specific locations, as well as the production and exudation of camalexin. Lately, Kopriva *et al.* [36] identified gene *CYP71A27* encoding an uncharacterized cytochrome P450 that contributes to camalexin biosynthesis and to interactions between the plant and root microbes. The *CYP71A27* loss-of-function mutant affected not only the microbial sulfatase activity in the rhizosphere but also interactions with introduced plant growth-promoting bacterial strains. Work by Salas-González *et al.* [37\*\*] further demonstrated that the genes regulating root diffusion barriers influence the composition of the plant microbiota, and reciprocally that microbes colonizing the root influence the functioning of root diffusion barriers. Microbial metabolites that can affect root system architecture up close and from a distance are the volatile organic compounds (VOCs) [38]. Recently, Moisan *et al.* [39] found that VOCs of a fungal root pathogen can also affect directional growth of roots. Using a root Y-tube olfactometer, they observed that directional growth was significantly affected but root length and root dry weight were not impacted by the directional ‘choice’ of the primary root. Collectively, these and other studies highlight that the reciprocal interactions between plant roots and their associated microbiomes can significantly shape the architecture of the MicrobiHome foundation.

### Establishing rooms

Plants can sense microenvironmental changes in the soil and respond to these by tailoring the growth and development of roots via, among others, altered branching, extension, placement and growth direction of roots. For common bean, Perez-Jaramillo *et al.* [40] revealed that the overall variation in rhizobacterial community composition was explained for 11.4% by root phenotypic traits, which represented most of the variation in rhizobacterial composition explained by the common bean genotype. They further showed that the abundance of Bacteroidetes families was higher on roots of wild common bean lines with a higher specific root length, whereas the abundance of Actinobacterial families was higher on roots of domesticated bean lines with a lower specific root length. Collectively, these results suggested a link between common bean domestication, specific root morphological traits and rhizobacterial community assembly. By documenting 11 root traits of 20 subarctic tundra meadow plant species and their rhizosphere microbial taxa and functional guilds, Spitzer *et al.* [41] recently found that high specific root lengths and small diameters of fine roots were associated with lower ratios of fungi:bacteria and Gram+:Gram– bacteria.

Figure 1



Current principles and techniques to design the MicrobiHome.

To build a MicrobiHome for beneficial microbes, there are four key points: i) constructing a stable foundation: in this stage, root exudates are important for root-soil interface friction mitigation, rhizosphere soil particles stabilization and re-organization, and recruitment of beneficial microbes; ii) establishing rooms: along the growing roots and among different types of roots (primary, lateral) differently sized soil pore networks are created that function as spatially separated niches ('rooms') for different root microbiome members. Reciprocally, microbiome members also can modify these root phenotypic traits; iii) gathering food: root exudates are the prime source of nutrients that nourish the microbes and influence microbiome assembly and functions; microbes possess versatile signal transduction systems to perceive and metabolize different nutrients; iv) communication: microbes communicate among and between each other, in part in a cell-density-dependent manner, via diverse diffusible compounds and VOCs. These compounds function as infochemicals in short and long-distance communications. To achieve the above proposed key points, diverse integrated strategies are discussed. We propose to design 'smart roots' with 'extended root phenotypes and genotypes' by connecting plant genetics to plant microbiome taxonomy and functions to guide future breeding strategies for elite crops. In addition, we highlighted the importance and up-to-date advances of experimental evolution approaches, including self-assembled communities, to generate adaptive beneficial plant microbiomes.

These effects of root traits on microbial composition are most likely determined, in part, by the differently sized pore networks along the growing roots that function as spatially separated niches ('rooms') for different root microbiome members. By using X-ray CT scans, Helliwell *et al.* [42,43] observed that pore structural changes in the rhizosphere were not uniformly distributed along the root. Juyal *et al.* [44] further showed that, at a soil bulk-density of 1.6 g/cm<sup>3</sup>, the average number of *Pseudomonas* and *Bacillus* cells was more than 60% lower than at a soil bulk-density of 1.3 g/cm<sup>3</sup>. Microbial composition along the growing roots is not only determined by root traits but also by microbial traits such as cell size, motility, attachment and enzymatic activities [45,46,47]. For example,

Kravchenko *et al.* [45] found higher activities of microbial enzymes such as chitinase, beta-glucosidase, and xylanase associated with 30–150 μm soil pores than for pores smaller than 30 μm. The authors suggested that pore size of 30–150 μm allow a good water and oxygen supply for resident microbial communities, whereas smaller pores tend to have longer periods of anoxia [48,49]. Hence, the diversity of soil pore sizes along roots generates differently sized 'rooms' that affect the rhizosphere microbiome quantitatively and qualitatively.

In addition to these 'mechanical' processes that create spatial niches for microbial colonization, also other factors are playing a role in creating spatially distinct

micro-habitats, such as exudate heterogeneity along the growing root and interactions between the plant immune system and microbiota members. For example, Yu *et al.* [50] showed that plant growth-promoting *Pseudomonas capeferrum* WCS358 and *Pseudomonas simiae* WCS417 could repress root immune responses of *Arabidopsis thaliana* via lowering environmental pH by the production of gluconic acid. This exemplifies the ability of introduced microbiome members to successfully colonize a given host and to create a niche to persist. To date, however, our current knowledge of spatial preference and heterogeneity in colonization patterns by community members (particularly on/in the root) is still largely elusive in relation to the concept of spatial (or temporal) niche building. Phenotyping technologies using labeled strains as well as mutant libraries will greatly help to visualize and mechanistically disentangle spatial colonization patterns of introduced microbial strains or SynComs. For instance, via mariner-based transposon insertion sequencing (INSeq), Wheatley *et al.* [51] elegantly discovered genetic determinants for rhizobial colonization of spatially discrete microhabitats in the root of pea. Similar approaches can conceivably be used to obtain similar information for other commensal microbial genera and even small synthetic consortia.

### Living inside the MicrobiHome

#### Gathering food

Once the MicrobiHome is established with taxonomically and functionally different ‘rooms’, other processes such as nutrient acquisition and communication need to be considered. Root exudates represent the major nutrient source for carbon-limited microbes in the rhizosphere and these exudates vary both quantitatively and qualitatively along the growing root [52,53]. Badri *et al.* [54] were among the pioneers to demonstrate the impact of changes in root chemistry on microbiome assembly. *Arabidopsis* mutants disrupted in the ABC transporter *abcg30* showed increased exudation of phenolics, decreased secretion of sugars and a less diverse bacterial community. Additionally, accumulation of phenolic compounds in poplar seedlings silenced in the cinnamoyl-CoA reductase (CCR) led to distinct community structure and functions of the endosphere microbiome [55]. Hu *et al.* [56] further showed that indole-derived benzoxazinoids (BXs) released by maize roots in the surrounding soil influenced even the microbiome composition of the next generation of maize plants growing in that same soil. Using untargeted mass spectrometry in combination with prokaryotic and fungal amplicon sequencing, Cotton *et al.* [57] revealed that BXs regulate global root metabolism and concurrently influence the root microbiome in a root type-dependent manner. They further revealed a dominant role for BXs-dependent metabolites, particularly flavonoids, in constraining a range of soil microbial taxa while stimulating methylophilic bacteria. Along the

same lines, Huang *et al.* [58\*\*] identified cocktails of triterpenes released by *Arabidopsis* roots that modulate root microbiome assembly. The recent study by Vilchez *et al.* [59] added yet another level of complexity by showing the role of epigenetic mechanisms in exudate-mediated microbial recruitment. More specifically, they showed for *Arabidopsis* and tomato, that active DNA demethylation regulates the production of the root exudate *myo*-inositol. Root-secreted *myo*-inositol was shown to preferentially attract *Bacillus megaterium* among the examined bacterial species and was critical for root colonization by plant growth-promoting *B. megaterium* strain YC4. Mechanistically, Stringlis *et al.* [60] showed the involvement of the root-specific transcription factor MYB72 of *Arabidopsis* in the exudation of the coumarin scopoletin, an iron-mobilizing phenolic compound that adversely affected growth of root pathogenic fungi but not the growth of a plant growth-promoting *Pseudomonas*. They further hypothesized that beneficial rhizobacteria ‘join forces’ with plants thereby improving ‘niche establishment for the microbial partner and growth and immunity benefits for the plant’. Furthermore, Harbort *et al.* [61] investigated the impact of coumarin secretion on the root microbiota in soils with different mineral nutrient availability and the consequences for plant productivity. Using wild type *A. thaliana* Col-0 and mutants in coumarin biosynthesis or export, shoot fresh weight and leaf chlorophyll content of the mutants decreased in iron-limiting soil, which indicated the importance of coumarin biosynthesis for plant growth. Microbiome analysis demonstrated that coumarin biosynthesis affected community assembly, with a reciprocal beneficial function provided by community members to the plant host via iron mobilization. In line with this, Korenblum *et al.* [62] referred to the mechanism by which the rhizosphere microbiome affects root exudation as ‘systemically induced root exudation of metabolites’ (SIREM). The authors showed that local colonization by rhizobacteria, for example, *Bacillus* and *Pseudomonas*, can trigger systemic exudation of acylsugars and glycosylated azelaic acid.

To further exemplify the complexity of the molecular and chemical interplay between plants and root microbes, a number of studies have suggested that plants under attack by insect or fungal pathogens change their exudation profile to attract beneficial microbes that can help suppressing the primary infection, preventing secondary infections or minimizing infections in the next generation of the same plant species. This phenomenon of ‘cry for help’ was elegantly dissected in a recent review by Rolfe *et al.* [63] providing several lines of evidence, albeit largely circumstantial, that plants can activate, via changes in root exudation, beneficial members within the microbiome to provide short-term or long-term protection. Being able to respond to these chemical changes in root exudates and to consume or degrade specific



exudate constituents requires specific signal transduction systems [64] and transporters (presumably inducible) [65]. In this context, Levy *et al.* [66] showed, through computational approaches, that plant-associated bacteria possess more genes for signal transduction and carbohydrate transport than bulk soil bacteria. Chemotaxis receptors were identified for *B. subtilis* and *B. amyloliquefaciens* for sensing sugars such as galactose and mannose [67,68] and a large variety of amino acids [68,69]. Moreover, many bacteria use active motility, via extracellular appendages or secreted metabolites, to disperse over small spatial scales up or down gradients of resources or attractants [70]. So far, however, relatively few bacterial model species are being studied to unravel the mechanisms of active dispersal, including swimming, swarming, gliding, twitching, and sliding [71,72]. To fully understand microbial behaviour in the chemically heterogeneous micro-environments in the rhizosphere, it will be necessary to integrate structural and chemical imaging through modelling these processes at the pore-scale [73–76]. The obtained fundamental knowledge can then be adopted for the design of crops with enhanced secretion of specific exudates that recruit beneficial microbes and/or that trigger beneficial microbial activities at the right time and place.

#### Communication with the neighbors

In soil and rhizosphere environments, microbes communicate via diffusible chemical signals, in particular quorum sensing (QS) molecules, where cell-to-cell distances are 10–20  $\mu\text{m}$  [77,78]. Gram-negative bacteria use acylhomoserine lactones (AHLs) as communication signals [79], whereas Gram-positive bacteria use oligopeptides [80]. Also the molecule c-di-AMP can play a role in interbacterial cell–cell communication in plant microbiomes [81]. Recently, Finkel *et al.* [82\*\*] elegantly demonstrated how interactions between microbes influence root growth. Using SynComs with different compositional complexity, they showed that a single bacterial genus (*Variovorax*) can reverse the inhibition of *Arabidopsis* root growth induced by a complex SynCom. They further showed that without *Variovorax*, the SynComs induced root morphological changes via auxin-dependent and ethylene-dependent pathways. Moreover, the authors identified the auxin-degrading *iac* operon in *Variovorax* and showed its involvement in the degradation of the plant growth-hormone indole-acetic acid produced by other rhizobacteria in the SynCom.

Microbes produce various other metabolites that can function as antimicrobials or serve as signaling compounds among the same or different species. For example, Lozano *et al.* [83] showed that the purple antibiotic violacein produced by *Chromobacterium violaceum* ATCC 31532 was induced by hygromycin A from *Streptomyces* sp. 2AW. Via binary interactions of 224 bacterial strains isolated from the *A. thaliana* phyllosphere, a new

antibiotic namely macrobrevin was found produced by a *Brevibacillus* sp. Leaf182 strain [84]. Translocation of various microbial metabolites requires continuous liquid phases in the rhizospheric soil matrix, whereas VOCs can translocate through air-filled and gas-filled soil pores and act as an attractant or repellent of other microorganisms in long-distance communication [85,86]. For example, Schulz-Bohm *et al.* [87] showed that specific VOCs can diffuse in soil over a distance of even 12 cm. Meanwhile, the authors showed the attraction of bacterial strains by VOCs emitted from roots of the grass *Carex arenaria* infected by *Fusarium culmorum*. If and how this long-distance communication via root-emitted VOCs impacts on the temporal and spatial composition and gene expression in the whole root microbiome is not yet known. As discussed above, the pore geometry and air-water interfaces will play critical roles in the diffusion, exchange and activity of these signaling molecules, and hence affect social interactions within and between microbial communities and their host plant. Although most of these mechanistic studies on communication among root-associated microorganisms have so far been conducted *in vitro* or in controlled bioassays with single plant species, Kong *et al.* [88\*] recently demonstrated that the composition of the rhizosphere microbiota in neighboring plants may be synchronized through plant VOCs. They showed that inoculation of tomato plants with root-colonizing *B. amyloliquefaciens* strain GB03 resulted in high similarity of microbial communities of the neighboring plants. This synchronization appeared to be associated with emission of the VOC  $\beta$ -caryophyllene from the leaves of inoculated tomato plants, which in turn elicited the release of salicylic acid in roots of the neighboring plant. Also in the field of plant ecology, it is well established that symbionts can play a role in plant-plant interactions and plant community dynamics. For example, the study by Fitzpatrick *et al.* [89] showed that differences in microbiota composition/preference among angiosperms affects plant performance through plant-soil feedback.

Another important aspect to consider is the ability of microbial consortia to persist and compete in the environment with the indigenous (soil-microbiota and plant-microbiota) microbiota. In this context, we can learn from the strategies fungal root pathogens use to invade the rhizosphere and penetrate the root tissues. An intriguing example of this was described recently for the promiscuous fungal root pathogen *Verticillium dahliae* that conditionally secretes an array of antimicrobial peptides that modulate soil microbiota for its own advantage [90]. Furthermore, Carlström *et al.* [91] showed that also priority effects are critical during the establishment of SynComs in the phyllosphere. These examples illustrate that identifying traits that allow introduced microbes or SynComs to successfully invade, establish and survive in interactions with the existing indigenous microbiota is the key to success in the design of

### Box 1 Future perspectives for building a beneficial MicrobiHome

#### Breeding crops with extended root phenotypes and genotypes

For designing crops with specific root traits, we propose here breeding 'smart roots' with a root architecture that not only benefits the crops with increased nutrient and water use efficiencies, but that also generates versatile soil porosity that maximizes the microbial functionalities [92\*]. Breeding crops with desired secondary metabolites/exudates using metabolic engineering and synthetic biology approaches could be another approach for building a beneficial MicrobiHome. Knowledge of root exudation chemistry of plants under siege can be used in plant breeding strategies or alternatively in artificial exudate media or reactors enriched with 'cry for help' metabolites to assemble beneficial microbiomes that confer enhanced biotic stress tolerance in crops [63]. The latter approach of self-assembled microbiomes was recently proposed for designing microbiomes that confer enhanced nutrient acquisition [93]. In the context of engineering crops with a balanced and 'desired-to-produce' root exudation profile, Tian *et al.* [94] recently proposed that re-domestication of current cultivated crops is the key to future crop design. To this end, it is crucial to understand if and how domestication has led to a depletion of specific plant traits (such as root exudation) that are essential in the recruitment and/or activation of beneficial microorganisms.

To simulate, at least in part, the environment of a beneficial MicrobiHome, different technologies have been or are being developed: i) Schaffner *et al.* [95] designed a 3D printing platform that enables additive manufacturing of complex 3D living architectures of bacteria-laden hydrogels with full localization and concentration control of bacteria. With the freedom of shape provided by this printing technique and the inherent diverse metabolic activity of bacteria, materials with unprecedented functionalities along different roots can be created, adding a new dimension to 3D printing; ii) Microfluidic technology to create microbial habitat structures [96,97] can be explored to increase environmental realism by incorporating structures at the micro- to nanometer scale that confine microorganisms and prevent unintended cellular dispersal and diffusion of substrates or signaling molecules; iii) Artificial soil aggregates [98] or 'transparent soil' [99,100] with conglomerates of soil particles of different sizes can be mimicked by imprinting arrays of cylinders or walls with varying diameters and shapes, simulating soil porosity, aggregation and surface roughness.

#### Experimental evolution of beneficial microbiomes

A challenging approach to engineer microbiomes with beneficial, adaptive and long-lasting effects is experimental evolution. Mueller *et al.* [101] developed a method to propagate evolving microbiomes during plant-microbiome interactions by using a non-evolving, highly inbred plant population. Furthermore, they used low carbon soil to increase the strength of host-control mediation of microbiome assembly and microbiome persistence. With this repeated passaging method, they artificially selected for rhizosphere microbiomes that confer salt-tolerance to the model grass *Brachypodium distachyon*. In line with this, Jochum *et al.* [102] selected rhizosphere microbiomes of wheat with repeated cycles under drought condition. As indicated above, also Morella *et al.* [12\*\*] successfully selected for a plant microbiome that is robust after colonization of target hosts. These studies demonstrated the changes of microbiome composition during targeted experimental evolution. Next to this, also evolution of members of the microbiome *in situ* was observed. Li *et al.* [103] experimentally showed that within six successive growth cycles of *Arabidopsis*, *Pseudomonas protegens* CHAO evolved from an initially deleterious root-associated bacterium into a mutualist. In another study with a year-long evolution experiment of five inoculations of the bacterium *Ensifer meliloti* on the host plant *Medicago truncatula* showed that the evolved microbes are more beneficial as reflected by the increased shoot biomass and higher number of nodules [104\*]. Collectively, these studies showed that microbes are able to rapidly adapt and develop a more beneficial relationship with their host plants.

Next to this, it is important to recapitulate the ecological conditions that select for the natural assembly of a microbial community with a desired function. Environmental parameters such as C:N:P ratios, oxygen concentrations, trace elements, primary carbon sources and secondary metabolites may be used to steer diazotrophic community assembly. Given these parameters, different reactor types (attached versus suspended growth), mode of operation (batch, fed batch or continuous), and process parameters (hydraulic retention time, solid retention time and particle size distribution) may be used to further control community assembly. Therefore, ecological theory and process engineering should be integrated to generate 'self-assembled' microbiomes enriched for particular beneficial functions related to plant growth promotion, nutrient acquisition or disease suppression, and adapted to a specific target environment [93]. To this end, experimental approaches can be used that are similar to that of Chen *et al.* [105] for remodeling the mouse gut microbiome toward the low-fat-diet state.

environmentally robust engineered microbiomes with desired features.

### Conclusion highlight

Plant roots define not only the composition of the soil microbial community, but, by creating soil pores, also create spatial patterns of microhabitats that affect the root microbiome both quantitatively and qualitatively. Here, we presented different views and approaches on how to design a 'home' for beneficial microbiome. The various intriguing and new technologies presented will hopefully inspire new investigations into the importance of microscale interactions between plants, microbes and environment for macro-scale (landscape) characteristics of terrestrial ecosystems and for the design of new strategies in sustainable crop production (Box 1).

### Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgements

We are grateful to Prof. Jeff Dangl and Prof. Jonathan Jones for inviting us to write this review. We thank Dr Jingjing Peng and Dr Wei Qin for their inspiring discussions and suggestions on this article. This work has received funding from the National Natural Science Foundation of China (31902112), China Scholarship Council (No. 201913043), the Program of Advanced Discipline Construction in Beijing (Agriculture Green Development), and the 2115 Talent Development Program of China Agricultural University to CS. This work has received funding from China Scholarship Council (No. 201913043), the Program of Advanced Discipline Construction in Beijing (Agriculture Green Development) and the 2115 Talent Development Program of China Agricultural University to KJ. The contribution of JMR was funded by the Dutch NWO Gravity program Microp (<https://www.microp.org>). The figure of this article was Created with BioRender.com.

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- of special interest
- of outstanding interest

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